Behavioral/Systems/Cognitive

A Regret-Induced Status Quo Bias

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A suboptimal bias toward accepting the status quo option in decision-making is well established behaviorally, but the underlying neural mechanisms are less clear. Behavioral evidence suggests the emotion of regret is higher when errors arise from rejection rather than acceptance of a status quo option. Such asymmetry in the genesis of regret might drive the status quo bias on subsequent decisions, if indeed erroneous status quo rejections have a greater neuronal impact than erroneous status quo acceptances. To test this, we acquired human fMRI data during a difficult perceptual decision task that incorporated a trial-to-trial intrinsic status quo option, with explicit signaling of outcomes (error or correct). Behaviorally, experienced regret was higher after an erroneous status quo rejection compared with acceptance. Anterior insula and medial prefrontal cortex showed increased blood oxygenation level-dependent signal after such status quo rejection errors. In line with our hypothesis, a similar pattern of signal change predicted acceptance of the status quo on a subsequent trial. Thus, our data link a regret-induced status quo bias to error-related activity on the preceding trial.

Introduction

When faced with a complex decision, people tend to accept the status quo. Indeed, across a range of everyday decisions, such as whether to move house or trade in a car, or even whether to flip the TV channel, there is a quantifiable tendency to maintain the status quo and refrain from acting (Samuelson and Zeckhauser, 1988). We previously investigated neural mechanisms for overcoming such a status quo bias in a difficult perceptual task (Fleming et al., 2010), but we did not address why the bias might arise in the first place. One influential view is that the status quo bias is associated with anticipated regret (Baron and Ritov, 1994), with the status quo bias reflecting a regret-minimizing strategy, as described below. Here, we explore how asymmetric behavioral and brain responses for errors after rejecting, or accepting, a status quo option may be associated with a status quo bias on subsequent decisions.

Decisions to reject a status quo are considered less normal, and less easily justified, than decisions to accept it (Kahneman and Miller, 1986; Connolly and Zeelenberg, 2002). This allows for easier construction of counterfactual alternatives, thus amplifying the associated emotional response, including feelings of regret from any resulting error (Kahneman and Tversky, 1982; Landman, 1987; Baron and Ritov, 1994; Feldman et al., 1999; Tsiros and Mittal, 2000). Status quo rejection may also be perceived as more directly causal of its outcome, enhancing a sense of accountability for an error (Ritov and Baron, 1990; Spranca et al., 1991). Indeed, an amplified experience of regret following a mistaken status quo rejection is proposed to underlie a behavioral

bias toward accepting the status quo in later decisions (Baron and Ritov, 1994). The status quo bias may also provide a means of regulating future regret, by improving the perceived justifiability of future choices (Zeelenberg and Pieters, 2007).

Motivated by the literature connecting regret and a status quo bias, we examined the bias's underlying neural mechanisms, linking choice behavior and neuronal activity at choice to antecedent error processing. Functional neuroimaging studies report a critical role for medial prefrontal cortex (mPFC) and insula in error processing (Carter et al., 1998; Braver et al., 2001; Menon et al., 2001). Similar regions have been implicated in negative choice evaluation and regret (Liu et al., 2007; Chua et al., 2009), as has the orbitofrontal cortex (OFC) (Camille et al., 2004; Coricelli et al., 2005; Chandrasekhar et al., 2008). Finally, the insula is proposed to be a region that predicts future consequences (Critchley et al., 2001; Preuschoff et al., 2008; Singer et al., 2009) and may be involved not only in representing outcomes of choices, but also in how such information guides future behavior. This background literature led us to predict that activity in one or more of these regions is associated with an enhanced emotional response to status quo rejection errors.

Materials and Methods

Participants. Twenty healthy individuals participated. All were right-handed with normal or corrected-to-normal vision (determined by self report). Three participants were excluded after equipment failures meant their responses were not fully recorded during scanning. Thus, 17 participants in all were included in our data analysis (eight female, mean age, 23.5 ± 4.8 years). Participants provided informed consent in accordance with UCL Research Ethics Committee approved procedures. Twenty additional participants were included in an initial manipulation-check behavioral experiment (15 female, mean age, 22.8 ± 4.0 years).

Experimental procedure. We modified a task reported by Fleming et al. (2010), designed to assess neuronal mechanisms associated with status quo rejection, by adding explicit trial-by-trial performance feedback (Fig. 1) for errors and correct responses. In brief, the task requires a trial-by-trial perceptual decision, with participants judging whether a target ball, landing on a simulated tennis court, was "IN" (overlapping

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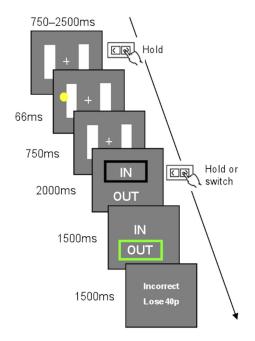


Figure 1. An exemplar trial timeline. Participants began each trial holding the key corresponding to their choice on the previous trial, while fixating on the central cross flanked by two tramlines. After a varied delay, a ball landed on either the left or right of the screen, at any height on the tramline. Participants were then asked to judge whether the ball landed IN (overlapping the line) or OUT. Their decision was indicated by either continuing to depress their previous decision (a black box served to remind them of this status quo), or to switch to the alternative key to reject the status quo and switch their decision. On rejecting the status quo, participants then held the new key until they chose to switch again on a later trial. Accuracy feedback and associated monetary win or loss was presented at the end of each trial.

the line) or "OUT". Participants started each trial by holding the key corresponding to their choice on the previous trial (for the first trial, participants started by holding IN). Each trial began with a central fixation cross and two peripheral lines. After a variable delay, the target ball appeared briefly (66 ms) on either the left or right of the screen. Since the side of target presentation was random, participants were instructed to fixate centrally to maximize performance on the task, although formal eye-tracking was not instigated as it was irrelevant to our experimental question. Participants were then reminded of their previous choice (the key currently still pressed, either IN or OUT), and had to decide either to continue holding the current key to stay with their previous choice (accept status quo) or to switch to the alternative key, thus switching their decision (reject status quo). Participants then held the appropriate key (new if they had switched, old if they had not) until the occurrence of a trial in which they chose to switch.

To create a balanced design, the correct decision was to accept the status quo on 50% of trials and to reject the status quo on the remaining 50%. Explicit feedback was presented at the end of each trial, corresponding to a 40 p gain or loss for correct or incorrect decisions, respectively. To obtain \sim 30% errors overall, we manipulated the difficulty of the perceptual decisions by altering the distance of the target from the outside edge of the line, using a 2-up-1-down staircase procedure (Levitt, 1971) in steps of 0.1 degrees of visual angle. Participants made an average of 100.24 errors over the course of 320 trials. There was a mean of 37.53 status quo rejection errors and 62.71 status quo acceptance errors. Overall, each participant played 320 trials over four separate sessions, while fMRI brain data were simultaneously acquired in the main experiment. Keys were pressed with the index or middle finger of the right hand, and key-choice contingencies (i.e., whether index or middle meant IN or OUT) were counterbalanced across sessions. Participants were paid according to the actual winnings for their two best sessions, which averaged £25.51 in the main experiment (SD = £2.7).

After scanning, participants provided subjective ratings of experienced regret in response to errors in the task. These were *post hoc* overall ratings

(not trial-by-trial) taken outside the scanner and based on a nine-point Likert scale. Participants rated relative regret for status quo rejection versus acceptance errors, as well as absolute regret for overall errors (i.e., collapsing across accept and reject errors). For relative regret ratings, they were asked "Which felt more regretful: when you stayed with your previous choice and made an error or when you switched your choice and made an error?" Ratings were also given for feelings of absolute and relative disappointment.

In an initial manipulation-check experiment, using an identical behavioral task performed outside the scanner, a separate cohort of participants rated their experienced regret on a scale of 1 to 9 after every error trial, where 9 was the highest level of possible regret. This additional experiment sought to confirm that errors on the task did indeed induce reported experiences of regret, while also aiming to obtain unique evidence for a trial-by-trial account of the rejection-acceptance differences in regret (since previous studies had largely relied on anticipated relative regret for hypothetical scenarios, rather than actual personal current experiences of regret). Skin conductance was acquired in this additional experiment, as described previously (Bach et al., 2009), using 8 mm Ag/AgCl cup electrodes and 0.5%NaCl gel on thenar/hypothenar of the nondominant hand. Constant voltage was provided by a custom-build coupler, and data were recorded using a 1401 signal converter and spike software (Cambridge Electronics Design). The skin conductance data were z-transformed and analyzed using dynamic causal modeling as described previously (Bach et al., 2010). Each trial onset, ball appearance, decision cue, and outcome were modeled as separate events, each followed by a fitted evoked skin conductance response (SCR) with a canonical shape (Bach et al., 2011). The task used in this manipulation-check was otherwise the same as in the scanning study.

Imaging acquisition. We scanned participants in a 3T Trio whole-body scanner (Siemens) operated with its standard body transmit and 12channel head receive coil. The manufacturer's standard automatic threedimensional-shim procedure was performed at the beginning of each experiment. Participants were scanned with a single-shot gradient-echo EPI sequence, optimized to reduce blood oxygenation level-dependent (BOLD) sensitivity losses in the orbitofrontal cortex due to susceptibility artifacts (Weiskopf et al., 2006). Imaging parameters were as follows: 48 oblique transverse slices tilted by 30°; slice thickness, 2 mm with a 1 mm gap between slices; repetition time (TR), 3.36 s; $\alpha = 90^{\circ}$; echo time (TE), 30 ms; bandwidth in the phase-encoding direction, 27 Hz/pixel; positive phase-encoding gradient polarity in an anterior-posterior direction; field of view, 192×192 mm²; matrix size, 64×64 ; fat suppression; z-shim gradient prepulse moment, -1.4 mT/m×ms. EPI data acquisition was monitored on-line using a real-time reconstruction and quality assurance system (Weiskopf et al., 2007). We acquired field maps for each subject at the start of scanning (Siemens standard double echo gradient echo field map sequence; TR, 10.2 ms; TE, 12.46 ms; matrix size, 64×64 ; 64 slices covering the whole head; voxel size, $3 \times 3 \times 3$ mm). These allowed calculation of static geometric distortions caused by susceptibility-induced field inhomogeneities, which were used to correct EPI images for both these static distortions and any changes in these distortions due to head motion (Andersson et al., 2001; Hutton et al., 2002). We also recorded heart rate with a pulse oximeter, along with respiratory phase and volume using a breathing belt; the recordings were used to correct for physiological noise during data analysis. At the end of the scanning session, we acquired a T1-weighted anatomical scan for each participant using a modified driven equilibrium Fourier transform sequence (Uğurbil et al., 1993), with optimized parameters as described previously (Deichmann et al., 2004). For each volunteer, 176 sagittal partitions were acquired with an image matrix of 256 \times 224 (read \times phase).

Behavioral analyses. In our manipulation-check behavioral experiment, we tested for a difference between experienced regret ratings for rejection and acceptance errors, using a paired-sample t test. Ratings were z-scored to remove individual differences in mean regret ratings. Post hoc (rather than on-line) ratings of subjective response to errors were analyzed in the scanning experiment. These included absolute ratings of regret and disappointment in response to errors overall. Relative responses to rejection and acceptance errors were collected along the

same dimensions, and a mean bias for one type of error over the other was tested with a one-sample *t* test against the null hypothesis of no bias (midpoint rating of 5 on the Likert scale).

As regards behavioral choice in the tennis-line perceptual judgment task, we predicted an overall status quo bias (a tendency to accept the previously chosen option) in line with what has been shown for this particular line judgment task (Fleming et al., 2010). We measured such bias as a tendency toward accepting the previous choice over and above what was the correct (optimal) choice on each trial, assessed with a t test. We also measured how this status quo bias was influenced by the outcome of the preceding trial, using a 2×2 repeated-measures ANOVA on choices in the current trial, with factors for outcome (correct, incorrect) and choice (accept, reject) in the previous trial.

Imaging preprocessing and analysis. Image preprocessing and data analysis were implemented using Statistical Parametric Mapping software in Matlab2009a (SPM8; Wellcome Trust Centre for Neuroimaging at UCL). After discarding the first six volumes of each session to allow for T1 equilibration, EPI images were corrected for geometric distortions caused by susceptibility-induced field inhomogeneities. Field maps were processed for each participant using the FieldMap toolbox implemented in SPM5 (Hutton et al., 2004). The EPI images were then realigned and unwarped using SPM8 (Andersson et al., 2001). Each participant's structural image was then coregistered to the mean of the motion-corrected functional images using a 12-parameter affine transformation, and segmented according to the standard procedure in SPM8 (Ashburner and Friston, 2005). The spatial normalization parameters resulting from the previous step were then applied to the functional images to allow for intersubject analysis, and finally these images were smoothed using an 8 mm full width at half maximum Gaussian kernel, in accord with the standard SPM approach.

In this experiment, we used fMRI to test two hypotheses in relation to the link between error type and the status quo bias. First, guided by the regret literature (see Introduction, above), we tested the prediction that error-related brain responses would be greater for erroneous status quo rejection than for erroneous status quo acceptance. Since the overall main effect of rejection error compared with acceptance error would be confounded by the motor response (changed or unchanged key), we tested instead for the critical interaction between outcome (error/correct feedback) and status quo rejection/acceptance. Specifically, for the BOLD data corresponding to the feedback event, we tested the following contrast: reject status quo (error – correct) > accept status quo (error – correct). This contrast was performed within an event-related general linear model using a model that included our four main regressors of interest: accept-error, accept-correct, reject-error, and reject-correct. Onsets were modeled with stick-functions at the time of feedback outcome and convolved with the standard canonical hemodynamic response function in SPM8 and its temporal derivative. Regressors of no interest comprised target ball onsets and button press, along with start of the decision phase parametrically modulated by reaction time (RT) if a decision to reject the status quo was made. This modulation by RT was included to factor out activity previously shown to reflect variations in task difficulty (Fleming et al., 2010). Head motion parameters defined by the realignment procedure were entered as six regressors of no interest, along with 17 additional regressors of cardiac phase (10 regressors), respiratory phase (six regressors), and respiratory volume (one regressor).

We generated statistical parametric maps from contrasts of interest. At the time of outcome feedback, we were interested in the main effect of error corrected for multiple comparisons across the whole brain volume. For the critical outcome-related two-way interaction, reject (error – correct) > accept (error – correct), we restricted our search volume to a functional region of interest (ROI) defined using the orthogonal main effect of error > correct (mask extent threshold, p < 0.005 uncorrected). Within these ROIs, we report voxelwise activity significant at a family-wise error (FWE) corrected threshold of p < 0.05. For completeness, we also report activity that survived whole-brain cluster-wise corrected significance of p < 0.05.

Our second main hypothesis was that differences in the processing of erroneous (vs correct) status quo rejection versus acceptance would be associated with an increased behavioral status quo bias on the subsequent trial. Specifically, we tested for two forms of a three-way interaction whereby enhanced responsivity to status quo rejection, compared with status quo acceptance, errors [i.e., reject (error - correct) > accept (error - correct) in the fMRI data] should be associated with a subsequent behavioral decision to accept (rather than reject) the status quo. We hypothesized that such an interaction could be associated either with outcome-driven brain responses on the preceding trial (predicting subsequent choice on the next trial) or with choice-driven brain responses (associated with the initiation of the actual choice on the next trial). To test whether asymmetries in error processing could underlie a behavioral status quo bias in either of these ways, we implemented two further event-related general linear models per participant. The first modeled onsets at the time of outcome feedback (for the four outcome types: accept-error, accept-correct, reject-error, and reject-correct) contingent on the choice made on the subsequent trial (subsequent accept or subsequent reject). The second modeled onsets at the start of the subsequent decision phase, for either reject status quo or accept status quo choices on the current trial contingent on outcome type in the previous trial. In both models, onsets were stick functions convolved with a canonical hemodynamic response function and its temporal derivative. Motion and physiological regressors of no interest were as in the previous model. We generated statistical parametric maps from the three-way interaction contrast of interest. For both models, we restricted our analysis to functional ROIs identified from the outcome-related effects found in the first model. The same statistical thresholds were used, as described above.

Results

Manipulation-check behavioral study

Our preliminary behavioral experiment showed trial-by-trial regret ratings with a mean of 5.83 of 9. Critically, regret ratings were greater for reject status quo errors (mean = 6.00; *z*-scored mean = 0.09) than accept status quo errors (mean = 5.66; *z*-scored mean = -0.06) ($t_{(19)} = 2.21$, p < 0.05), in line with previous studies. Here, we uniquely extend this finding to actual trial-by-trial outcomes and personal experiences, rather than hypothetical scenarios as in previous studies. Overall, we found a significant 6.2% bias toward accepting, rather than rejecting, the status quo ($t_{(19)} = 5.01$, p < 0.0001). We also observed an effect of correctness in skin conductivity response at the time point of outcome, where the SCR was bigger for incorrect than for correct responses ($t_{(20)} = 2.9$, p < 0.01). No effect was observed for rejecting the status quo, nor for the interaction of this with correctness, on SCRs.

fMRI experiment

Post hoc subjective ratings

As predicted, regret was significantly greater for reject status quo errors than accept status quo errors (mean deviation from no bias = 1.24, $t_{(16)}$ = 2.32, p < 0.05). No such effect was found for ratings of disappointment (mean deviation from no bias = 0.35, $t_{(16)}$ = 0.63, p values, not significant).

fMRI data: enhanced response to status quo rejection errors in anterior insula and mPFC

We examined BOLD signals aligned to the time of outcome feedback. A main effect of error > correct was found in bilateral anterior insula (Fig. 2a) (p < 0.05, whole brain cluster-level corrected; height threshold. p < 0.001). No effect of error was found within the OFC. The opposite contrast, correct > error responses, revealed effects in striatum, postcentral gyrus, superior temporal cortex, and superior occipital cortex (p < 0.05, whole brain cluster-level corrected), but are of less interest because of the lack of a priori hypotheses for our purposes.

We next performed the critical interaction contrast to determine whether the main effect of error (vs correct) was greater for

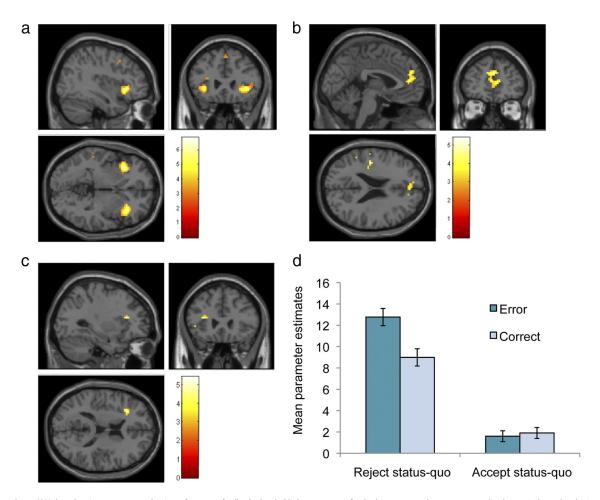


Figure 2. Group SPM data showing responses at the time of outcome feedback, thresholded at p < 0.005 for display purposes, shown on a normalized canonical template brain. a, Bilateral anterior insula response to the main effect of error > correct (MNI peaks -36, 17, -5 and 39, 26, -2). b, Whole brain corrected activity in medial prefrontal cortex (MNI peak 3, 47, 25) reflecting the interaction of choice and outcome [reject (error > correct) - accept (error > correct)]. c, d, Anterior insula activity from the main effect of error, showing the same interaction of choice and outcome (c) and the plotted mean parameter estimates for the four outcome types at the peak voxel (MNI -30, 26, 16) (d). Error bars show within-subject SEs of the difference between error and correct responses for the two decision types.

reject status quo errors than for accept status quo errors, in line with the subjective ratings. We again tested for activity corresponding to outcome feedback. At whole-brain cluster-level corrected significance, we found that activity in medial prefrontal cortex (extending into the rostral anterior cingulate) showed greater responsivity to reject errors compared with accept errors (Fig. 2b). Additionally, we tested whether error-related activity in anterior insula, within a mask defined by the (orthogonal) main effect of error (extent threshold, p < 0.005), showed greater activity for reject compared with accept errors. We found left anterior insula activity was significantly greater for reject status quo than to accept status quo errors (p < 0.05, FWE corrected for the ROI) (Fig. 2*c*,*d*). No regions showed significant effects for the inverse interaction. We tested whether these responses in the insula and mPFC depended on stronger ratings of experienced regret in the participants, and found no significant effects of individual variation in experience within these brain regions. This raises questions for how closely these responses relate to the conscious experience of regret, especially since error-related responses in mPFC may not be associated with awareness of the error (Hester et al., 2005; O'Connell et al., 2007). It is also possible that this null between-subject effect may be due to a lack of sensitivity in the postscan emotional ratings for picking up trial-by-trial brain responses. All effects are summarized in Table 1.

Table 1. Activation for the main effects of error and correct trials and the interaction of outcome with rejecting or accepting the status quo

Brain regions	MNI coordinates of local maxima	Voxel number at $p < 0.001$ uncorrected	Voxel t
Error > correct			
L anterior insula (BA 47)	-36, 17, -5	68	6.89
R anterior insula	39, 26, − 2	69	6.44
Superior frontal (BA 8)	3, 32, 52	11	5.88
Correct > error			
R postcentral	36, -31, 64	133	6.59
R superior temporal (BA 41)	57, -22, 10	121	6.42
R putamen	21, 8, -8	23	6.06
R superior occipital (BA 19)	30, -85, 25	61	5.97
R supplementary motor area	12, -16, 73	50	5.50
R paracentral lobule (BA 6)	3, -37, 61	193	5.30
R caudate	27, 2, 13	43	5.21
Reject (error > correct) — accept (error > correct)			
Medial prefrontal cortex/anterior	2 47 25	4.4	476
cingulate (BA 9)	3, 47, 25	14	4.76
L anterior insula	−30, 26, 16	3	4.62

Contrasts were performed on responses modeled at the time point of trial outcome feedback. R, Right; L, left; BA, Brodmann area.

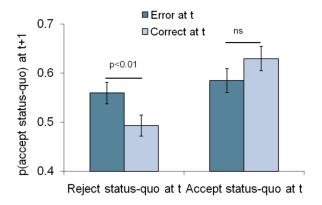


Figure 3. Figure illustrates how the status quo bias is contingent upon the outcome of the previous trial. Error bars show within-subject SEs of the difference between error and correct responses for the two decision types. ns, Not significant.

Anterior insula and mPFC activity at choice predicts the status quo bias

In our main scanning experiment, we observed a 7.9% status quo bias ($t_{(16)} = 7.59$, p < 0.00001). We tested whether this bias related to the outcome of the previous trial, using a 2×2 repeated-measures ANOVA with factors of outcome (error/correct) and reject/accept status quo on the previous trial. We found a main effect of reject/accept, such that overall participants tended to repeat the strategy used on the previous trial (i.e., to keep rejecting or keep accepting, $F_{(1,16)}=13.79, p<0.005$). This effect interacted with outcome ($F_{(1,16)}=11.25, p<0.005$), with erroneous status quo rejection encouraging greater subsequent status quo acceptance (mean probability = 0.56) compared with correct status quo rejection (mean probability = 0.49) ($t_{(16)}$ = 3.15, p < 0.01), which was not the case for erroneous (mean probability = 0.59) compared with correct status quo acceptance (mean probability = 0.62; $t_{(16)} = -1.88$, not significant) (Fig. 3). Furthermore, erroneous rejection of the status quo was the only outcome type that drove a tendency toward an alternative strategy (i.e., from rejection to acceptance of the status quo, or viceversa) on the subsequent trial, as shown by a one-sample t test against no bias ($t_{(16)} = -3.21$, p < 0.01).

At the time of choice on the subsequent trial, pooling correct and error trials, we found enhanced brain activity associated with a decision to reject the status quo (compared with accept) in bilateral cerebellum, bilateral supramarginal gyrus, and bilateral insula (p < 0.05, whole-brain cluster-level corrected). Decisions to accept the status quo were associated with a trend significant cluster in rostral anterior cingulate cortex (ACC) (p < 0.06, FWE corrected).

We next explored the possible link between enhanced errorrelated activity following rejection errors and a behavioral bias toward subsequent status quo acceptance. Accordingly, we designed a three-way interaction contrast which tested whether the critical two-way interaction [reject (error - correct) > accept (error - correct)] was associated with participants making a subsequent decision to accept rather than to reject the status quo, thereby linking a neural response and a subsequent behavioral status quo bias. We found significant effects when modeling the interaction at the time of subsequent choice. Specifically, we found that an anterior insula response in the previously described orthogonal two-way interaction was expressed when participants choose to accept the status quo on the next trial but not when they decide to reject the status quo (contrast estimates at coordinates MNI - 30, 26, 16 taken forward to a $2 \times 2 \times 2$ ANOVA, threeway interaction, $F_{(1,16)}=10.51$, p<0.005). mPFC showed a similar pattern to anterior insula, such that an enhanced responsivity to errors under status quo rejection was also expressed at subsequent choice, but only when participants chose to accept rather than reject the status quo. However, this response was not expressed within the same peak as for the two-way outcomerelated response. These choice-related responses are shown in Figure 4 and in supplemental Table S1 (available at www. jneurosci.org as supplemental material).

When the three-way interaction was tested at the time of preceding outcome (instead of during subsequent choice as above), now recategorized by subsequent choice, no significant effects were found. Our time course plots in Figure 4, b and d, also indicate these brain responses appear to emerge at the time of choice on the subsequent trial. Since a three-way interaction was not identified in these regions at the time of preceding outcome, these results suggest a choice-related fMRI response (arising on the next trial but dependent on the outcome of the previous trial). We note, however, that the limited intertrial interval and low temporal resolution of fMRI leads to some caution in exact temporal assignment of the BOLD signal. Future studies exploiting the higher temporal resolution of magnetoencephalography may be useful for teasing apart the temporal dynamics of outcomedriven versus choice-driven responses in the status quo bias.

Discussion

We previously reported a status quo bias for difficult perceptual decisions (Fleming et al., 2010), but those findings did not account for why, in situations of uncertainty, participants are driven to stay with a status quo rather than change to a different option. Here, we hypothesized that erroneous rejection of the status quo may lead to greater regret than erroneous acceptance of the status quo, both psychologically and neurobiologically, and that such an asymmetry is a key driver of status quo biases. Greater regret after status quo rejection may reduce its justifiability and appeal, thus encouraging future decisions that align with a status quo option.

In keeping with this perspective, we show erroneous status quo rejection is associated with stronger feelings of regret than erroneous status quo acceptance, with anterior insula and mPFC BOLD signals also showing an inflated error response specifically for erroneous status quo rejections (as opposed to erroneous status quo acceptance). Both regions are implicated in error processing (Carter et al., 1998; Menon et al., 2001; Ullsperger and von Cramon, 2004; Klein et al., 2007), but hitherto without consideration of status quo rejection versus status quo acceptance. A particular role of the anterior insula in interoceptive awareness and subjective feeling states (Craig, 2002; Critchley et al., 2002, 2004) has shaped theories of insula involvement in detection of external threat stimuli or loss, and in awareness of ensuing physiological arousal. Errors that people become aware of are associated with stronger insula activity compared with those of which they are unaware, in keeping with an increased autonomic response with the former (Klein et al., 2007), whereas responses in the mPFC do not typically depend upon awareness of the error (Hester et al., 2005; O'Connell et al., 2007).

We found no evidence for increased physiological arousal, as assessed with SCRs for status quo rejection versus status quo acceptance errors. Although null outcomes for SCRs should be interpreted with caution, we did find significant effects for error versus correct feedback overall, but no selectivity for status quo acceptance versus rejection. This hints that the anterior insula status quo-related activity represents more than mere physiolog-

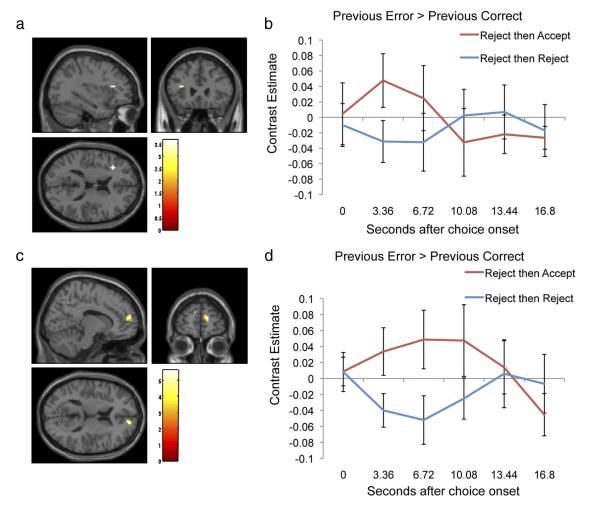


Figure 4. Group SPM data showing responses at the time of subsequent choice, thresholded at p < 0.005 for display purposes, shown on a normalized canonical template brain. a, b, Anterior insula activity reflecting an interaction of previous choice and outcome with current choice (MNI -30, 26, 16) [i.e., reject (error - correct) > accept (error - correct) only when the current choice is to accept). c, d, The same three-way interaction within medial prefrontal cortex (peak MNI 15, 56, 13).

ical arousal. Despite psychological literature consistently showing that errors stemming from decisions to reject a status quo are not experienced as equivalent to those stemming from a decision to accept a status quo, to our knowledge the present study is the first to address error processing in the brain in terms of such differences. The fact we did not find OFC involvement in such responses is surprising, given its putative role in regret (Camille et al., 2004; Coricelli et al., 2005; Chandrasekhar et al., 2008). However, recent studies have provided no evidence for a role of OFC in the experience of regret (Nicolle et al., 2010, 2011), although others have shown a greater role of the anterior insula in such experiences (Chua et al., 2009).

Our participants showed a clear overall bias toward accepting the status quo. Previous literature suggests that past experience of higher regret for status quo rejection errors encourages higher anticipated regret for the prospect of similar status quo rejection errors in the future (Ritov and Baron, 1990, 1995; Baron and Ritov, 1994; Kordes-de Vaal, 1996; Tykocinski and Pittman, 1998, 2001; Tykocinski et al., 2004). Amplified emotional and neuronal responses to erroneous status quo rejection, compared with status quo acceptance, as identified for the first time here, could lead decision-makers to consider accepting the status quo as the more justifiable future choice (Connolly and Zeelenberg, 2002; Inman and Zeelenberg, 2002; Zeelenberg et al., 2002).

Here, we found such a decision bias to be associated with activity in the anterior insula and mPFC, regions which also show an inflated response to status quo rejection errors at the time of a similar preceding outcome.

Existing evidence suggests the insula is involved in processing information necessary for learning and motivated behavior (e.g., risk and uncertainty) (Paulus et al., 2003; Huettel et al., 2006; Preuschoff et al., 2008). The insula is also implicated in anticipation of future aversive outcomes, which is important for avoidance learning (Ploghaus et al., 1999). It is reported to play a role in both fear and anxiety (Shin and Liberzon, 2010), in a perceived increase in the probability of future aversive events, post-error behavioral modification, and response slowing (O'Doherty et al., 2003; Paulus et al., 2003; Kuhnen and Knutson, 2005; Paulus and Stein, 2006; Hester et al., 2007; Clark et al., 2008). Singer et al. (2009) have outlined a functional model of the insula that postulates a role in integrating internal physiological and external sensory information, along with their associated uncertainty, contextual information, and individual preferences, to motivate adaptive subsequent behavior. Our results are in keeping with a role of the insula in post-error behavioral adaptation, in this case encouraging a status quo bias in response to previously amplified emotional (and neuronal) responses to erroneous status quo rejection. However, others have provided evidence for a greater role

of the anterior cingulate, rather than the insula, in error anticipation and avoidance (Magno et al., 2006). Although the activity reported by Magno et al. (2006) is in more posterior ACC than what we report in mPFC, it nevertheless raises a question as to the respective roles of the mPFC and insula in a regret-induced status quo bias, where the former may be involved in anticipation of future regret in response to an error, and the other may be involved in a regret-avoidant behavioral response.

In this and in our previous study (Fleming et al., 2010), a status quo bias and an inaction bias (i.e., decision not to act) are synonymous by design. It is unclear whether an inaction bias and a status quo bias are independent or are driven by the same underlying cause (Ritov and Baron, 1992; Baron and Ritov, 1994; Schweitzer, 1994; Anderson, 2003). In particular, the potential for regret may be a driving force behind both biases, so the two might be considered a unitary construct for the purpose of this study. It remains possible that an inaction bias arises primarily, or exclusively, at the level of the motor response, with the effort needed to act or switch behavior a salient feature in driving the asymmetric impact of erroneous decisions to accept and reject the status quo. Status quo biases, on the other hand, may arise at the more abstract level of the decision, with features such as the normality and perceived causality of the behavior playing a greater role. Future research could address possible differences in the way inaction and status quo biases are processed in the brain. Regret aversion may also mediate the effect of decision conflict on a status quo bias. For example, a regret-averse preference for normality may explain a commonly observed tendency to revert to familiar strategies in complex reasoning tasks (the Einstellung effect) (Bilalić et al., 2008, 2010). Future studies could address possible interactions between a regret-induced status quo bias and level of decision conflict.

In conclusion, we suggest that an inflated emotional and neurobiological response to status quo rejection errors (compared with status quo acceptance errors) is a key contributor to the emergence of a status quo bias. In support of this, we show enhanced error-related responses in anterior insula and mPFC, as well as enhanced subjective feeling of regret, for status quo rejection errors. The observed asymmetries in neural and emotional responses predict a bias toward the status quo in subsequent decision making.

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